though with a difference, to the conceptions of Cuvier, to those numerous and relatively sudden revolutions of the surface of the globe which have produced the corresponding dynasties in its succession of inhabitants.

THE FUTURE

The work of a systematic paleontologist, especially of one dealing with rare and obscure fossils, often seems remote from the thought and practice of modern science. I have tried to show that it is not really so. But still it may appear to some to have no contact with the urgent problems of the world outside. That also is an error. Whether the views I have criticized or those I have supported are the correct ones is a matter of practical importance. If we are to accept the principle of predetermination, or of blind growth-force, we must accept also a check on our efforts to improve breeds, including those of man, by any other means than crossing and elimination of unfit strains. In spite of all that we may do in this way, there remain those decadent races, whether of ostriches or human beings, which "await alike the inevitable hour." If, on the other hand, we adopt the view that the life-history of races is a response to their environment, then it follows, no doubt, that the past history of living creatures will have been determined by conditions outside their control, it follows that the idea of human progress as a biological law ceases to be tenable; but, since man has the power of altering his environment and of adapting racial characters through conscious selection, it also follows that progress will not of necessity be followed by decadence; rather that, by aiming at a high mark, by deepening our knowledge of ourselves and of our world, and by controlling our energy and guiding our efforts in the light of that knowledge, we may prolong and hasten our ascent to ages and to heights as yet beyond prophetic vision.

HEREDITY

By Miss E. R. SAUNDERS

PRESIDENT OF THE BOTANICAL SECTION

BY the term Inheritance we are accustomed to signify the obvious fact of the resemblance displayed by all living organisms between offspring and parents, as the direct outcome of the contributions received from the two sides of the pedigree at fertilization: to indicate, in fact, owing to lack of knowledge of the workings of the hereditary process, merely the *visible*

consequence—the final result of a chain of events. Now, however, that we have made a beginning in our analysis of the stages which culminate in the appearance of any character, a certain looseness becomes apparent in our ordinary use of the word Heredity, covering as it does the two concomitant essentials, genetic potentiality and somatic expression—a looseness which may lead us into the paradoxical statement that inheritance is wanting in a case in which, nevertheless, the evidence shows that the genetic constitution of the children is precisely like that of the parents. When we say that a character is inherited no ambiguity is involved, because the appearance of the character entails the inheritance of the genetic potentiality. But when a character is stated not to be inherited it is not thereby indicated whether this result is due to environmental conditions, to genetic constitution, or to both causes combined. That we are now able in some measure to analyze the genetic potentialities of the individual is due to one of those far-reaching discoveries which change our whole outlook and bring immediately in their train a rapidly increasing array of new facts, falling at once into line with our new conceptions, or by some orderly and constant discrepancy pointing a fresh direction for attack. A historical survey of the steps by which we have advanced to the present state of our knowledge of Heredity has so frequently been given during the last twenty years that the briefest reference to this part of my subject will suffice.

The earliest attempts to frame some general law which would coordinate and explain the observed facts of inheritance were those of Galton and Pearson. Galton's observations led him to formulate two principles which he believed to be capable of general application—the Law of Ancestral Heredity and the Law of Regression. The Law of Ancestral Heredity was intended to furnish a general expression for the sum of the heritage handed on in any generation to the succeeding offspring. Superposed upon the working of this law were the effects of the Law of Regression, in which the average deviation from the mean of a whole population of any fraternal group within that population was expressed in terms of the average deviation of the parents. These expressions represent statements of averages which, in so far as they apply, hold only when large numbers are totaled together. They afford no means of certain prediction in the individual case. These and all similar statistical statements of the effects of inheritance take no account of the essentially physiological nature of this as of all other processes in the living organism. They leave us unenlightened on the fundamental

question of the nature of the means by which the results we witness came to pass. We obtain from them, as from the melting-pot, various new products whose properties are of interest from other viewpoints, but, corresponding to no biological reality, they have failed to bring us nearer to our goal—a fuller comprehension of the workings of the hereditary mechanism. Progress in this direction has resulted from the opposite method of inquiry—the study of a single character in a single line of descent, the method which deals with the unit in place of the mass. The revelation came with the opening of the present coloring matter anthocyanin in the petals of plants such as the stock and sweet pea. Our proof that two factors (at least) are here involved is obtained when we find that two true breeding forms devoid of color yield colored offspring when mated together. In this case the two complementary factors are carried, one by each of the two crossed forms. When both factors meet in the one individual, color is developed. We have in such cases the solution of the familiar, but previously unexplained, phenomenon of Reversion. Confirmatory evidence is afforded when among the offspring of such cross-bred individuals we find the simple 3 to 1 ratio of the one-factor difference replaced by a ratio of 9 to 7. Similarly we deduce from a ratio of 27 to 37 that three factors are concerned, from a ratio of 81 to 175 four factors, and so on. The occurrence of these higher ratios proves that the hereditary process follows the same course whatever the number of factors controlling the character in question.

And here I may pause to dwell for a moment upon a point of which it is well that we should remind ourselves from time to time, since, though tacitly recognized, it finds no explicit expression in our ordinary representation of genetic relations. The method of factorial analysis based on the results of interbreeding enables us to ascertain the least possible number of genetic factors concerned in controlling a particular somatic character, but what the total of such factors actually is we can not tell, since our only criterion is the number by which the forms we employ are found to differ. How many may be common to these forms remains unknown. In illustration I may take the case of surface character in the genera *Lychnis* and *Matthiola*. In *L. vespertina* the type form is hairy; in the variety *glabra*, recessive to the type, hairs are entirely lacking. Here all glabrous individuals have so far proved to be similar in constitution, and when bred with the type give a 3 to 1 ratio in F_2.[1] We speak of hairiness in this case, therefore, as being a

[1] Report to the Evolution Committee, Royal Society, I., 1902.

one-factor character. In the case of *Matthiola incana v. glabra*, of which many strains are in cultivation, it so happened that the commercial material originally employed in these investigations contained all the factors since identified as present in the type and essential to the manifestation of hairiness except one. Hence it appeared at first that here also hairiness must be controlled, as in *Lychnis*, by a single factor. But further experiment revealed the fact that though the total number of factors contained in these glabrous forms was the same, the respective factorial combinations were not identical. By interbreeding these and other strains obtained later, hairy F_1 cross-breds were produced giving ratios in F_2 which proved that at least four distinct factors are concerned.[2] Whereas, then, the glabrous appearance in *Lychnis* always indicates the loss (if for convenience we may so represent the nature of the recessive condition) *of one and the same factor*, analysis in the Stock shows that the glabrous condition results if *any factor out of a group of four* is represented by its recessive allelomorph. Hence we describe hairiness in the latter case as a four-factor character.

It will be apparent from the cases cited that we can not infer from the genetic analysis of one type that the factorial relations involved are the same for the corresponding character in another. That this should be so in wholly unrelated plants is not, perhaps, surprising, but we find it to be true also where the nature of the characteristic and the relationship of the types might have led us to expect uniformity. This is well seen in the case of a morphological feature distinctive of the N. O. Gramineæ. The leaf is normally ligulate, but individuals are occasionally met with in which the ligule is wanting. In these plants, as a consequence, the leaf blade stands nearly erect instead of spreading out horizontally. Nilsson-Ehle[3] discovered that in oats there are at least four and possibly five distinct factors determining ligule formation, all with equal potentialities in this direction. Hence, only when the complete series is lacking is the ligule wanting. In mixed families the proportion of ligulate to non-ligulate individuals depends upon the number of these ligule-producing factors contained in the dominant parent. Emerson[4] found, on the other hand, that in maize mixed families showed constantly a 3 to 1 ratio, indicating the existence of only one controlling factor.

[2] *Proc. Roy. Soc.*, B, Vol. 85, 1912.

[3] "Kreuzungsuntersuchungen an Hafer und Weizen," Lund, 1909.

[4] Annual Report of the Agricultural Experiment Station of the University of Nebraska, 1912.

From time to time the objection has been raised that the Mendelian type of inheritance is not exhibited in the case of specific characters. That no such sharp line of distinction can be drawn between the behavior of varietal and specific features has been repeatedly demonstrated. As a case in point and one of the earliest in which clear proof of Mendelian segregation was obtained, we may instance *Datura*. The two forms, *D. Stramonium* and *D. Tatula*, are ranked by all systematists as distinct species. Among other specific differences is the flower color. The one form has purple flowers, the other pure white. In the case of both species a variety *inermis* is known in which the prickles characteristic of the fruit in the type are wanting. It has been found that in whatever way the two pairs of opposite characters are combined in a cross between the species, the F_2 generation is mixed, comprising the four possible combinations in the proportions which we should expect in the case of two independently inherited pairs of characters, when each pair of opposites shows the dominant-recessive relation. Segregation is as sharp and clean in the specific character flower color as in the varietal character of the fruit. Among the latest additions to the list of specific hybrids showing Mendelian inheritance, those occurring in the genus *Salix* are of special interest, since heretofore the data available had been interpreted as conflicting with the Mendelian conception. The recent observations of Heribert-Nilson[5] show that those characters which are regarded by systematists as constituting the most distinctive marks of the species are referable to an extremely simple factorial system, and that the factors mendelize in the ordinary way. Furthermore, these specific-character factors control not only the large constant *morphological features*, but *fundamental reactions* such as those determining the condition of physiological equilibrium and vitality in general. In so far as any distinction can be drawn between the behavior of factors determining the varietal as opposed to the specific characters of the systematist, Heribert-Nilsson concludes that the former are more localized in their action, while the latter produce more diffuse results, which may affect almost all the organs and functions of the individual, and thus bring about striking alterations in the general appearance. *S. caprea*, for example, is regarded as the reaction product of two distinct factors which together control the leaf-breadth character, but which also affect, each separately and in a different way, leaf form, leaf color, height,

[5] "Experimentelle Studien über Variabilität, Spaltung, Artbildung und Evolution in der Gattung Salix," 1918.

and the periodicity of certain phases. We can not, however, draw a hard-and-fast line between the two categories. The factor controlling a varietal characteristic often produces effects in different parts of the plant. For example, the factors which lead to the production of a colored flower no doubt also in certain cases cause the tinging seen in the vegetative organs, and affect the color of the seed. Heribert-Nilsson suggests that fertility between species is a matter of close similarity in genotypic (factorial) constitution rather than of outward morphological resemblance. Forms sundered by the systematist on the ground of gross differences in certain anatomical features may prove to be more nearly related because the differentiating factors happen to control less conspicuous features.

THE SUPPLY OF OXYGEN TO THE TISSUES

By J. R. BARCROFT

PRESIDENT OF THE PHYSIOLOGICAL SECTION

PROMINENT among the pathological conditions which claimed attention during the war was that of insufficient oxygen supply to the tissues, or anoxæmia. For this there were several reasons; on the one hand, anoxæmia clearly was a factor to be considered in the elucidation of such conditions as are induced by gas poisoning, shock, etc. On the other hand, knowledge had just reached the point at which it was possible to discuss anoxæmia on a new level. It is not my object in the present address to give any account of war-physiology—the war has passed, and I, for one, have no wish to revive its memories, but anoxæmia remains, and, as it is a factor scarcely less important in peace than in war pathology, I think I shall not do wrong in devoting an hour to its consideration.

The object of my address, therefore, will be to inquire, and, if possible, to state, where we stand; to sift, if I can, the knowledge from the half-knowledge; to separate what is ascertained as the result of unimpeachable experiment from what is but guessed on the most likely hypothesis. In war it was often necessary to act on defective information, because action was necessary and defective information was the best that was to be had. In this, as in many other fields of knowledge, the whole subject should be reviewed, the hypotheses tested experimentally, and the gaps filled in. The sentence which lives in my mind as embodying the problem of anoxæmia comes from the